

# A REVISION OF *STENANDRIUM* (ACANTHACEAE) IN MEXICO AND ADJACENT REGIONS<sup>1</sup>

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## ABSTRACT

Nine species of *Stenandrium* Nees are recognized as occurring in the southern United States, Mexico, and northern Central America (Guatemala, Belize, El Salvador, Honduras, and Nicaragua). One of these species, *S. manchonense* T. F. Daniel from Guerrero, distinguished by its erect, caulescent habit and large, whorled leaves with undulate to angular margins, is described as new to science, and two new combinations, *S. nanum* (Standley) T. F. Daniel and *S. pilosulum* (Blake) T. F. Daniel, are made. *Stenandrium* is circumscribed in relation to its closest relatives, *Aphelandra* and *Holographis*. Each of the nine species is described, mapped, and distinguished from its relatives. Illustrations are provided for *S. manchonense*, *S. barbatum*, and *S. dulce*.

*Stenandrium* Nees is a genus of perennial herbs and subshrubs found in tropical and subtropical regions of the New World, from the southernmost regions of the United States to central Argentina and Chile. Over 50 species of *Stenandrium* have been described, largely from Brazil, the West Indies, and Mexico. The genus has not been the subject of any detailed study since Nees's treatment in DeCandolle's "Prodromus" (1847). Recent regional accounts of *Stenandrium* in North and Central America have been provided by Wasshausen (1966) for Texas and Gibson (1974) for Guatemala. Standley did not include an account of the genus in his treatment of Acanthaceae in "Trees and Shrubs of Mexico" (1926), undoubtedly due to the inconspicuousness of its woody nature.

During this study nine species were found to occur in Mexico. One of these is described as new to science and two new combinations in *Stenandrium* are made. Five of the species are endemic to Mexico. The range of *S. barbatum* extends into the western United States, and *S. pedunculatum* and *S. subcordatum* have ranges extending into northern Central America. These regions are covered by this revision for the sake of completeness. *Stenandrium dulce* has a broad geographic range, extending from the southern United States to Chile.

Vegetatively, plants of *Stenandrium* are often inconspicuous. Several of the species bear their leaves at or near ground level. Although these

plants are commonly referred to as acaulescent, they have an underground rhizome that bears a cluster of leaves at its apex. *Stenandrium barbatum* is somewhat intermediate between these acaulescent species and those with elongate, leafy stems. In this species the rhizomes frequently become aerial, although the leaves of the current season are typically clustered at their apices. In many individuals of *S. barbatum*, there is slight internodal elongation as well. Leaves of *Stenandrium* are either opposite or whorled depending on the species. The blades are usually entirely green and membranous in texture. In *S. nanum*, however, they have a pale green or whitish coloration along the major veins (also present in some individuals of *S. subcordatum*) and a coriaceous texture. The inflorescence consists of a lax to dense, bracteate spike. The bracts are green and vary from small (ca. 2.5 mm long) and subulate to large (ca. 21 mm long) and obovate. The flowers consist of a five-parted calyx and corolla, four short, monothecous stamens, an inconspicuous staminode, and a bicarpellate gynoecium. The corolla is inconspicuously bilabiate and the limb usually appears somewhat actinomorphic, or at least the lobes are all similar in form. Only in *S. subcordatum* is the corolla distinctly zygomorphic with the lobes of the upper lip conspicuously reduced in size relative to the lobes of the lower lip. The fruit is an ellipsoid capsule bearing four pubescent seeds.

Lindau (1895) placed *Stenandrium* in his

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subfamily Acanthoideae, tribe Aphelandreae, an assemblage of tropical American genera with a corolla imbricate in bud and with an upper lip, an androecium of four monothealous stamens, and tricolpate pollen. Bremekamp (1965) maintained this status for *Stenandrium* in his suggested revision of infrafamilial classification in the Acanthaceae. He noted that members of this tribe are distinguishable by a distinctly bilabiate corolla. This is not the case in *Stenandrium*, however, which usually has a subactinomorphic corolla suggestive of Bremekamp's Stenandriopsidae. Because infrafamilial classification in the Acanthaceae is unclear at the present time, no change in tribal status is suggested for *Stenandrium*.

The closest morphological relatives of *Stenandrium* that occur in the region covered by this revision are *Aphelandra* (Mexico through South America) and *Holographis* (endemic to Mexico). These three genera appear to be extremely closely related. In Mexico, where each genus has been thoroughly studied, they can be distinguished by the following key:

- 1a. Corolla subactinomorphic, the lobes more or less similar in form (or the upper lip considerably reduced in size with respect to the lower lip in *S. subcordatum*), the upper lip divided nearly to its base into two prominent, obovate lobes greater than 2.5 mm long; plants acaulescent (the leaves clustered at or near the ground) or caulescent; corolla pinkish or purplish (rarely white); anthers included in corolla tube; stigma funnelliform ..... *Stenandrium*
- 1b. Corolla zygomorphic, the lobes dissimilar in form, the upper lip entire to emarginate, or if bilobed with lobes greater than 2 mm long, the lobes not obovate and usually not more than one-half the length of the upper lip; plants caulescent; corolla yellow, orange, red, pinkish, purplish, or white; anthers usually partially or completely exerted from corolla tube; stigma bilobed or funnelliform.
  - 2a. Corolla red or yellow, 30–70 mm long; bracts conspicuous, 9–50 mm long, (3–)5–15 mm wide, often tinged with pink or purple and sometimes toothed ..... *Aphelandra*
  - 2b. Corolla yellow, pinkish, purplish, or white, 7–18 mm long; bracts inconspicuous, 1–5(–11) mm long, 0.5–2.5(–5) mm wide, green, entire ..... *Holographis*

It is evident from the above key that the distinctions among these genera are subtle at best. Although I believe all three genera should be maintained as such, mutually exclusive characters are not well developed among them. The characters and trends separating *Aphelandra* and

*Holographis* are discussed in more detail by Daniel (1983). The distinctions between *Stenandrium* and *Holographis* are further discussed by Daniel (1984). Despite their close relationship, *Stenandrium* and *Aphelandra* are usually readily distinguishable. The large, strongly zygomorphic corollas, usually well-exserted stamens, and conspicuous, often colored and/or toothed bracts of *Aphelandra* are not encountered in *Stenandrium*. Using these generic distinctions, however, several southern Central and South American species described in *Aphelandra* should be transferred to *Stenandrium*.

*Stenandrium* in the West Indies and South America has not been thoroughly studied yet. cursory examination of the 15 or so species described from the West Indies reveals that none of the species of the North and Central American mainland occur there. Indeed, all species known from the West Indies have been described as endemic to that region. Although I examined a limited amount of material from South America in order to better understand species circumscriptions and application of names, species from this region are also in need of further study. Because species from South America are so poorly known and the relationships among them and to the Mexican species are still largely undetermined, I have used a conservative species concept in this revision.

#### TAXONOMY

***Stenandrium*** Nees in Lindl., *Introd. Nat. Syst. Bot.*, 2nd edition, 444. 1836, nom. cons.  
 TYPE: *Stenandrium mandioccanum* Nees.

*Gerardia* L. *Sp. Pl.* 610. 1753, pro parte.

Acaulescent (arising from a woody rhizome or caudex) or caulescent perennial herbs or shrubs to 5 dm tall. Leaves opposite or whorled (4 per node), sessile or petiolate. Inflorescence of axillary or terminal, elongate or head-like, usually pedunculate spikes, the flowers sessile, subtended by 2 paired, isomorphic bractlets and a bract; bracts green, variable in shape, conspicuously ciliate in several species; bractlets subulate to linear to lanceolate. Calyx 5-lobed, the lobes divided nearly to the base, usually lance-subulate, equal or subequal in size; corolla pink, purple, or white, glabrous or pubescent on the outer surface (the trichomes sometimes restricted to the lower-central lobe), imbricate, the lower-central lobe outermost in bud, the tube cylin-

dric, apically ampliate into a short throat, the throat pubescent within, the limb bilabiate, 5-parted, appearing subactinomorphic to bilabiate, the upper lip bilobed, the lower lip trilobed, the lobes obovate, rounded to truncate at apex; androecium of 4 stamens and a staminode, the stamens subdidynamous, included, the filaments short (usually ca. 1 mm long), the anthers monothealous, pubescent, the staminode borne between the posterior pair of stamens, usually shorter than the filaments and lacking an anther;

pollen prolate to spheroidal, tricolpate (in ours as examined); style terminal, filiform, flared at apex into an asymmetrically funnelform stigma. Capsule ellipsoid, glabrous or pubescent. Seeds 4 (or fewer by abortion), laterally flattened, sub-oval in outline, the surface variously pubescent, the trichomes often with barbs, or branches.

*Distribution.* Southern North America (from about Lat. 33°N southward), West Indies, Central America, and South America.

KEY TO THE SPECIES OF *STENANDRIUM* IN MEXICO AND ADJACENT REGIONS

- 1a. Plants caulescent (internodal elongation clearly evident, the leaves not clustered at or near the ground level).
- 2a. Leaves whorled, 4 per node.
- 3a. Plants sprawling; leaves 6–14 mm long; peduncles 0.5–7 mm long; bracts 1–1.5 mm wide; calyx 5.5–8.5 mm long, the lobes purplish near apex ..... 1. *S. verticillatum*
- 3b. Plants erect; leaves 11–25 mm long; peduncles 20–110 mm long; bracts 1.5–2 mm wide; calyx 3.5–5.5 mm long, the lobes not purplish near apex ..... 2. *S. manchonense*
- 2b. Leaves opposite.
- 4a. Nodes callous; leaves coriaceous, the upper surface glabrous, pale green or whitish along major veins, the lower surface punctate-pitted; bractlets 0.7–1 mm wide ..... 3. *S. nanum*
- 4b. Nodes not callous; leaves membranaceous, the upper surface pubescent, concolorous, the lower surface not punctate-pitted; bractlets 0.3–0.7 mm wide.
- 5a. Leaves congested, vertical or nearly so, oblanceolate to spatulate, 2–9 mm wide; capsule 9–14 mm long; seeds 3–5.5 mm long, 2.5–4 mm wide; plants of the Chihuahuan Desert ..... 4. *S. barbatum*
- 5b. Leaves not congested, horizontal or spreading, ovate to elliptic to obovate, 7–45 mm wide; capsule 5.5–9(–13) mm long; seeds 1.5–3.5 mm long, 1–2.5 mm wide; plants occurring south of the Chihuahuan Desert.
- 6a. Bracts lance-subulate to subulate, 1–1.5 mm wide; seeds covered with rigid, papilla-like trichomes (rarely restricted to the margin) usually lacking branches or barbs ..... 5. *S. chameranthemoideum*
- 6b. Bracts obovate, 2.5–7(–12) mm wide; seeds covered with bristle-like trichomes bearing lateral barbs or branches ..... 6. *S. pedunculatum*
- 1b. Plants acaulescent (leaves clustered at or near the ground level).
- 7a. Bracts lance-subulate, 4.5–7 mm long, 0.5–1.5 mm wide; leaves truncate to cordate at base, not decurrent on the petiole ..... 7. *S. subcordatum*
- 7b. Bracts lanceolate to ovate to elliptic to obovate to strap-shaped, 6–21 mm long, 1.5–7.5 mm wide; leaves rounded to acute to attenuate at base, usually decurrent on the petiole, or plants leafless at anthesis.
- 8a. Leaf blades glabrous (although usually inconspicuously glandular along the basal portion of lower surface) or plants leafless at anthesis; bractlets linear to linear-lanceolate, tapering from above the middle if at all; capsule entirely pubescent; plants of the northern Sierra Madre Occidental ..... 8. *S. pilosulum*
- 8b. Leaf blades pubescent (rarely glabrous or only ciliate near base) at anthesis; bractlets subulate to lance-subulate, tapering from or below the middle; capsule glabrous or pubescent only above the middle; plants occurring east and south of the northern Sierra Madre Occidental.
- 9a. Internodes never elongated, plants strictly acaulescent, solitary; leaves spreading, ovate to elliptic (if oblanceolate or strap-shaped then 40–100 mm long and plants with peduncles 100–200 mm long), pubescent (rarely glabrous) with trichomes 0.2–1 mm long; seminal trichomes with flexuous or downward pointing lateral barbs or branches; plants not restricted to the Chihuahuan Desert ..... 9. *S. dulce*
- 9b. Internodes often with slight elongation evident, plants commonly forming dense mats; leaves vertical or nearly so, oblanceolate to spatulate (8–60 mm long and plants with peduncles 5–35 mm long), conspicuously pubescent with trichomes 1–4 mm long; seminal trichomes usually with conspicuously recoiled lateral barbs or branches; plants restricted to the Chihuahuan Desert ..... 4. *S. barbatum*

1. *Stenandrium verticillatum* Brandegee, Zoe 5: 237. 1906. TYPE: Mexico. Puebla: El Riego,

18°26'N, 97°24'W, July 1905, C. Purpus 1238 (holotype, UC!; isotypes, F!, GH!, MO!;

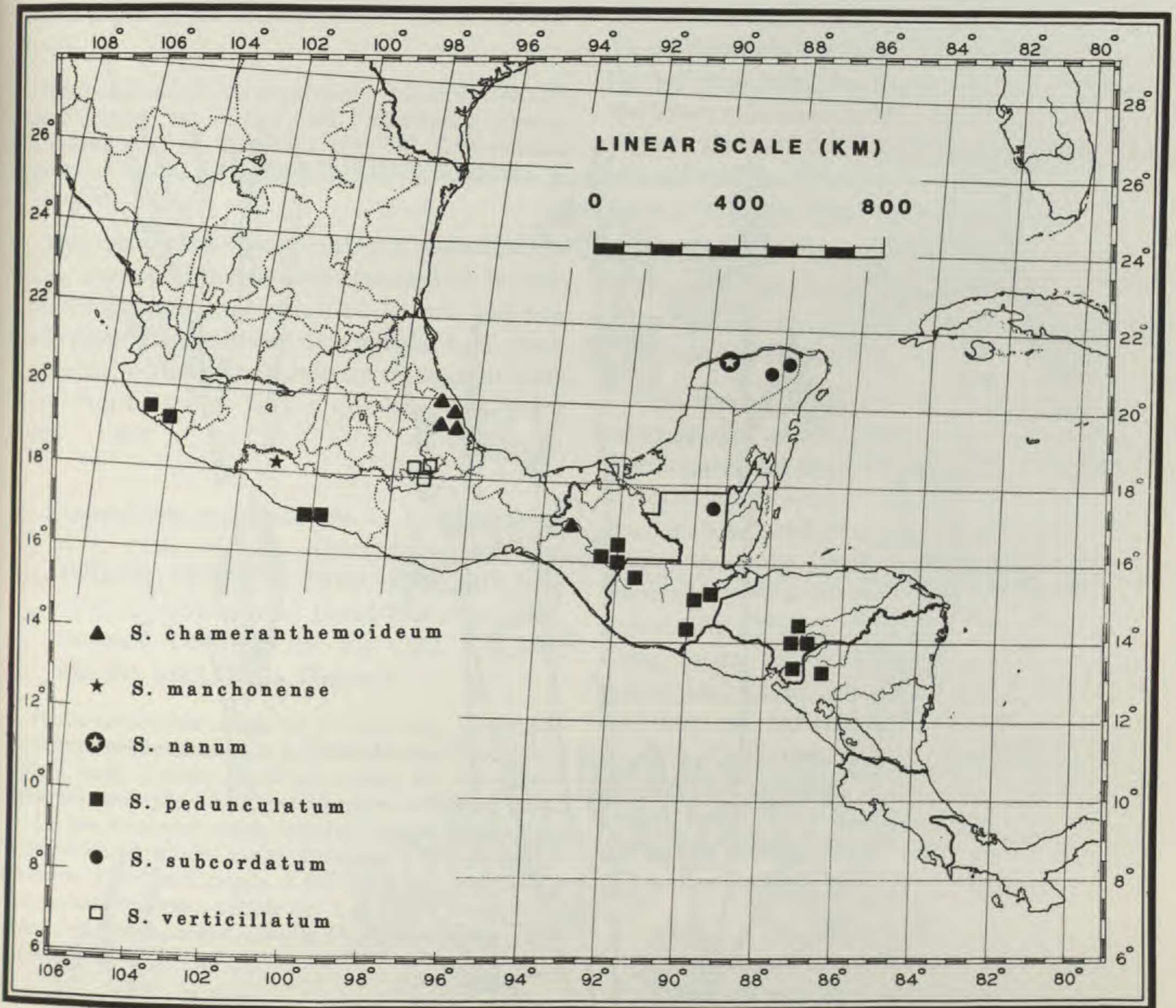


FIGURE 1. Distribution of *Stenandrium chameranthemoideum*, *S. manchonense*, *S. nanum*, *S. pedunculatum*, *S. subcordatum*, and *S. verticillatum*.

NY!, POM!, US!). *Gerardia verticillata* (Brandegge) Blake, Contr. Gray Herb. 52: 101. 1917.

Sprawling caulescent herb to 10 cm tall from a woody base. Stems subquadrate to terete, evenly pubescent with retrorse to flexuous trichomes 0.1–1.2 mm long. Leaves whorled, 4 per node, sessile to short-petiolate, the petioles 0.5–5 mm long, the blades obovate to elliptic to suborbiculate, 6–14 mm long, 4–7.5 mm wide, 1.2–2 times longer than wide (the lowermost leaves often reduced in size or scale-like), rounded to acute at apex, attenuate at base, the surfaces pubescent, the lower more densely so, the margin ciliate. Inflorescence of axillary or terminal, sessile or pedunculate spikes to 1.5 cm long, the peduncles 0.5–7 mm long, the spike axes pubescent like the stems; flowers opposite to subopposite along the

axes. Bracts lanceolate to lance-ovate, 4–7 mm long, 1–1.5 mm wide, pubescent like leaves. Bractlets linear to lance-subulate, 2–5.5 mm long, 0.5–0.8 mm wide, pubescent like leaves. Calyx 5.5–8.5 mm long, the lobes 5–8 mm long, purplish near apex, pubescent like leaves. Corolla rose-colored, 8–12 mm long, glabrous on outer surface, the tube 5–6 mm long, the upper lip 3–5 mm long with lobes 2.5–4 mm long, the lower lip 3–5.5 mm long with lobes 2.5–5 mm long. Stamens 1.5–2 mm long, the anthers 1.3–1.5 mm long. Capsules 7–8.5 mm long, sparsely pubescent to nearly glabrous; seeds 2.5–3 mm long, 2–2.5 mm wide, pubescent with bristle-like trichomes bearing lateral barbs or branches.

*Distribution.* Known only from the arid Tehuacán Valley (Fig. 1) of southern Mexico (Puebla and Oaxaca) where it was collected at eleva-



FIGURE 2. *Stenandrium manchonense*.—a. Habit.—b. Lower nodes showing scale-like leaves.—c. Upper node with whorled leaves.—d. Leaves showing variation in form.—e. Leaf apex.—f. Floral bud.—g. Flower.—h. Flower (side view).—i. Developing (immature) capsule.

tions between 2,000 and 2,700 meters (May–July).

*Additional specimens examined.* MEXICO, OAXACA: Los Naranjas, vic. of San Luis Tultitlanapa, Puebla, *C. Purpus* 3083 (F, GH, MO, NY, UC, US). PUEBLA: Cerro de Castillo, *C. Purpus* 2512 (UC); Acatitlán, *C. Purpus* 3939 (UC).

This species is known from four collections of *C. A. Purpus*. It can be distinguished by its low, sprawling habit, short whorled leaves, and apically purplish calyx lobes. It is similar to *S. manchonense*, with which it shares a caulescent habit and whorled leaves with a low length to width ratio.

2. *Stenandrium manchonense* T. F. Daniel, sp. nov. TYPE: Mexico. Guerrero: Manchón, 18°07'N, 100°59'W, Distr. Mina, 10 June 1937, *G. Hinton et al.* 10460 (holotype, US!; isotypes, DS!, ENCB!, F!, GH!, K!, LL!, MICH!, MO!, UC!). Figure 2.

Herba caulescens usque ad 2.5 dm alta; caules pubescentes trichomatibus 0.2–1 mm longis; folia verticillata, nodo quatuor, laminae ovatae vel suborbiculatae vel obovatae, 11–25 mm longae, 4–20 mm latae, 1–2.2-plo longiores quam latiores; inflorescentia spicata usque ad 11 cm longa; bracteae ovatae vel lanceolatae, 2.5–4 mm longae, 1.5–2 mm latae; bracteolae lanceolatae vel lanci-subulatae, 2–3.5 mm longae; calyx 3.5–5.5 mm longus; corolla 11–18 mm longa; capsula ignota.

Caulescent herb to 2.5 dm high. Stems subquadrate, pubescent with flexuous-crinkled trichomes 0.2–1 mm long. Leaves whorled, 4 per node, the lowermost leaves scale-like, sessile, elliptic to oblanceolate, 3–7 mm long, 2 mm wide, the upper leaves subsessile to short-petiolate, the petioles 0.5–3 mm long, the blades ovate to suborbiculate to obovate, 11–25 mm long, 4–20 mm wide, 1–2.2 times longer than wide, cuneate to attenuate at base, rounded to acute at apex, the margin ciliate, irregularly undulate, the undulations often somewhat angular, the surfaces pubescent. Flowers borne alternately in long-pedunculate, loose spikes to 21 cm long, the peduncles 2–11 cm long, the peduncles and rachis pubescent like the stems or the rachis lacking most of the longer trichomes. Bracts ovate to lanceolate, 2.5–4 mm long, 1.5–2 mm wide, the abaxial surface sparsely pubescent, the margin ciliate. Bractlets lanceolate to lance-subulate, 2–3.5 mm long, 0.5–0.8 mm wide, ciliate. Calyx 3.5–5.5 mm long, the lobes 3–5 mm long, sparsely pubescent to nearly glabrous on abaxial sur-

face, the margins ciliate. Corolla color unknown, 11–18 mm long, the tube 5–7 mm long, the upper lip 6–8 mm long, the lower lip 8–11 mm long, the lobes subequal (or the lobes of the upper lip slightly shorter), 6–9 mm long, glabrous on the abaxial surface. Stamens 1.5–2 mm long, the anthers 1–1.2 mm long. Capsules not seen.

*Distribution.* Known only from the type, which was collected in southwestern Mexico (Guerrero) in oak woods at an elevation above 1,100 meters (June) (Fig. 1).

This species is readily distinguished from all other species of *Stenandrium* by its erect, caulescent habit and relatively large (11–25 mm long), whorled leaves with an undulate to angular margin. Its closest relative appears to be *S. verticillatum*, the only other caulescent species with whorled leaves in Mexico. *Stenandrium verticillatum* differs from *S. manchonense* by its scrambling, bushy growth form, smaller leaves and bracts, and longer calyx with purplish lobes. In addition, the inflorescence of *S. verticillatum* consists of a short (to 1.5 cm), few-flowered spike that is either sessile or borne on a peduncle 0.5–7 mm long. In *S. manchonense*, the inflorescences are longer (3.5–21 cm), many flowered, and borne on peduncles 2–11 cm long.

3. *Stenandrium nanum* (Standley) T. F. Daniel, comb. nov. *Pseuderanthemum nanum* Standley, Publ. Field Columbian Mus., Bot. Ser. 8: 46. 1930. TYPE: Mexico. Yucatán: Silám, s.d., *G. Gaumer* 1305 (holotype, F!).

Caulescent perennial herb to 10 cm tall, from woody rhizome. Stems subquadrate, multi-striate, pubescent with straight trichomes 0.1–0.2 mm long, the nodes callous. Leaves opposite, petiolate, the petioles 3–6 mm long, pubescent like stem, the blades coriaceous, ovate to elliptic, 16–48 mm long, 10–27 mm wide, 1.6–2 times longer than wide, acute, sometimes unequal at base, acute to rounded at apex, the upper surface glabrous, pale green or whitish along the major veins, the lower surface punctate-pitted, with some trichomes along the midvein, the margin revolute. Inflorescence of axillary or terminal, sessile (or borne on peduncles to 1 mm long) spikes to 6 cm long. Bracts lanceolate, 6–7 mm long, 1.5 mm wide, pubescent like stem. Bractlets lanceolate, 4–5.5 mm long, 0.7–1 mm wide. Calyx 8–9 mm long, the lobes lance-subulate. Corolla 16–24 mm long, glabrous on outer surface,

the tube 8–14 mm long, the lobes of the upper lip 5–6.5 mm long, the lobes of the lower lip 7–9 mm long. Stamens 2 mm long, the anthers 1.5 mm long. Capsule 8–9 mm long, glabrous. Seeds not seen.

*Distribution.* Known only from two collections from the Yucatán Peninsula of Mexico (Fig. 1).

*Additional specimen examined.* MEXICO. YUCATÁN: Progreso, s.d., Gaumer 2295 (F).

Although Standley (1930) described this species in *Pseuderanthemum* and Leonard (1936) so maintained it, its proper position is in *Stenandrium*. Neither Standley nor Leonard discussed the androecial arrangement or capsular form of this species. In *Pseuderanthemum*, the androecium consists of two bitheous stamens containing tricolporate pollen and two staminodes and the capsule is stipitate. In *Stenandrium*, the androecium consists of four monotheous stamens with tricolpate (in ours as examined) pollen and the capsule lacks a stipe. Both specimens treated by Standley and Leonard have the diagnostic features of *Stenandrium*.

*Stenandrium nanum* is readily distinguished by the callous nodes and coriaceous leaves with a pale green or whitish coloration along the veins on the adaxial surface, and punctate-pitted abaxial surface. Its closest relative in Mexico appears to be *S. chamerantheroideum*. In addition to the above cited characters, it can be distinguished from *S. chamerantheroideum* by its longer, lanceolate bractlets and longer corollas. The ranges of these two species are not known to overlap.

4. *Stenandrium barbatum* Torr. & Gray, Pacific Rail. Rept. (Pope's Explor.) 2: 168. 1855. TYPE: United States. Texas: Pecos River, Mar. 1851, C. Wright 1453 (holotype, GH!; isotypes, GH!, K!, NY!). *Gerardia barbata* (Torr. & Gray) Blake, Contr. Gray Herb. 52: 100. 1917.

Dwarf acaulescent or subcaulescent perennial herb to 12 cm tall from a stout woody rhizome, often forming small, dense mats. Leaves vertically oriented, sessile or short-petiolate, the petioles to 5(–25) mm long, the blades oblanceolate to spatulate, 8–60 mm long, 2–5(–9) mm wide, (3–)4–11 times longer than wide, tapering-attenuate at base, acute at apex, pubescent with a sparse to dense understory of erect or bent trichomes 0.1–0.2 mm long and an overstory

(sometimes restricted to the margin) of flexuous trichomes 1–4 mm long, the margin entire. Inflorescence of leafy-bracteate, pedunculate spikes to 7 cm long, the peduncles to 35 mm long (not exceeding the leaves), pubescent with straight to retrorse trichomes 0.1–0.5 mm long and sometimes with flexuous trichomes 1–2 mm long as well, the spike axis pubescent with straight trichomes 0.1–0.2 mm long (sometimes very sparsely so), the flowers opposite to subopposite along the spike. Bracts oblanceolate to obovate to elliptic, 7–21 mm long, 2–4 mm wide, pubescent like the leaves. Bractlets subulate, 1.5–6 mm long, 0.3–0.6 mm wide, pubescent (sometimes sparsely so), usually with a mixture of eglandular trichomes and inconspicuous stipitate glands, the trichomes sometimes restricted to the margin and rarely consisting entirely of inconspicuous stipitate marginal glands. Calyx 4–8 mm long, the lobes subequal, lance-subulate, pubescent like bractlets. Corolla pinkish purple with white streaks on the lower lip, 13–21 mm long, glabrous or sparsely pubescent on the outer surface, the tube 4–5 mm long, the upper lip 5.5–9 mm long with lobes 4–8.5 mm long, the lower lip 6–11 mm long with lobes 6–9 mm long. Stamens 1.5–2 mm long, the anthers 1.5 mm long. Capsule 9–14 mm long, glabrous (rarely pubescent). Seeds 3–5.5 mm long, 2.5–4 mm wide, the testa densely pubescent with long, stiff, golden trichomes with usually conspicuously recoiled branches.

*Distribution.* Chihuahuan Desert regions of southern New Mexico, western Texas, eastern Chihuahua, and western Coahuila (Fig. 3) on limestone slopes and in arroyo gravel in desert associations of *Agave*, *Viguiera*, *Fouquieria*, *Larrea*, *Acacia*, *Dasyllirion*, *Prosopis*, and *Yucca* up to pinyon-juniper communities at elevations from 750 to 1,350 meters (Mar.–Oct.).

*Representative specimens examined.* UNITED STATES. NEW MEXICO: Chaves Co., ca. 2 mi. W of Roswell, Hinckley & Smith 4374 (SRSC); Doña Ana Co., 6 mi. W of El Paso, Hanson s.n. (TEX); Eddy Co., Carlsbad Caverns, Nelson 11402 (DS, GH, POM, UC); Lea Co., Monument, Castetter 70907 (UNM); Lincoln Co., 10 mi. NW of Riverside, Goodman & Waterfall 4958 (GH); Otero Co., Sacramento Mts., Van Deventer & Betancourt s.n. (ARIZ); Sierra Co., Elephant Butte Dam, Nelson 6122 (UNM). TEXAS: Brewster Co., Terlingua Beds, on rd. to Agua Frio Ranch from 118, Correll & Wasshausen 27843 (LL), 27897 (LL, UC); Culberson Co., Sierra Tinaja Pinta, San Antonio Peak, Correll & Rollins 23873 (ENCB, LL); El Paso Co., Franklin Mountains W of El Paso, Warnock 10328



FIGURE 3. Distribution of *Stenandrium barbatum*, *S. dulce*, and *S. pilosulum*.

(LL), Ferris & Duncan 2402 (CAS, DS), Lundell & Lundell 16940 (LL), Barlow s.n. (UC), Correll & Johnston 21834 (LL, UC), Daniel 2713 (ASU, MICH, NY); Hudspeth Co., near summit of Hueco Mountains, 30 mi. E of El Paso, McVaugh 8147 (CAS, DS, K, POM, TEX, UC); Jeff Davis Co., just W of Chispa summit, 30°43'N, 104°47'W, Johnston et al. 10684 (LL); Pecos Co., NE side of Sierra Madera, ca. 25 mi. S of Ft. Stockton, McVaugh 7914 (ASU, DS, TEX); Presidio Co., 2 mi. S of Shafter, Warnock 46642 (SRSC); Reeves Co., 16 mi. NW of Toyahvale, Rt. 290, Correll & Correll 38527 (ENCB, TEX); Terrell Co., 9½ mi. W of Dryden, Cory 43864 (GH, TEX). MEXICO. CHIHUAHUA: near Cd. Juarez, Pringle 8501 (ENCB, F, GH, K, MO, NY, POM, UC, US); ca. 9 mi. W of Ojinaga, Henrickson & Lee 15821 (TEX). COAHUILA: just across river from mouth of Maravillas Creek, Johnston et al. 10589.5J (LL); Sierra de las Cruces, vic. of Santa Elena Mines, Stewart 350 (GH, LL), 397 (LL).

*Stenandrium barbatum* is one of the better known and collected species due to its abundance in the United States and adjacent Mexico and its conspicuousness when in flower. The plants are usually copiously white hirsute and frequently form low, dense clumps with abundant pinkish purple corollas. Although the plants generally resemble other acaulescent species in habit, the

woody rhizomes of *S. barbatum* are frequently aerial and often branch. The leaves and inflorescences are often clustered at the branch apices; however, slight internodal elongation during the growing season commonly results in a short (to 15 mm long) stem. Because of this unusual situation and because of some intergradation between the leaves and bracts, *S. barbatum* is listed in the key under both initial leads.

The closest relatives of *S. barbatum* appear to be *S. dulce* and *S. pilosulum*. The close relationship between *S. dulce* and *S. barbatum* is illustrated by a specimen from western Coahuila (Stewart 397, LL) which is treated as *S. barbatum* because of its narrow, oblanceolate to spatulate leaves, long trichomes, and glabrous corolla lobes. However in several characters, including the lance-elliptic bracts on some individuals, and often sparse pubescence, this collection is suggestive of *S. dulce*, which also occurs in western Coahuila.

*Stenandrium barbatum* (Fig. 4) is readily distinguishable from both *S. dulce* and *S. pilosulum* by its dense, mat-forming habit, nearly vertical, oblanceolate to spatulate leaves that are con-



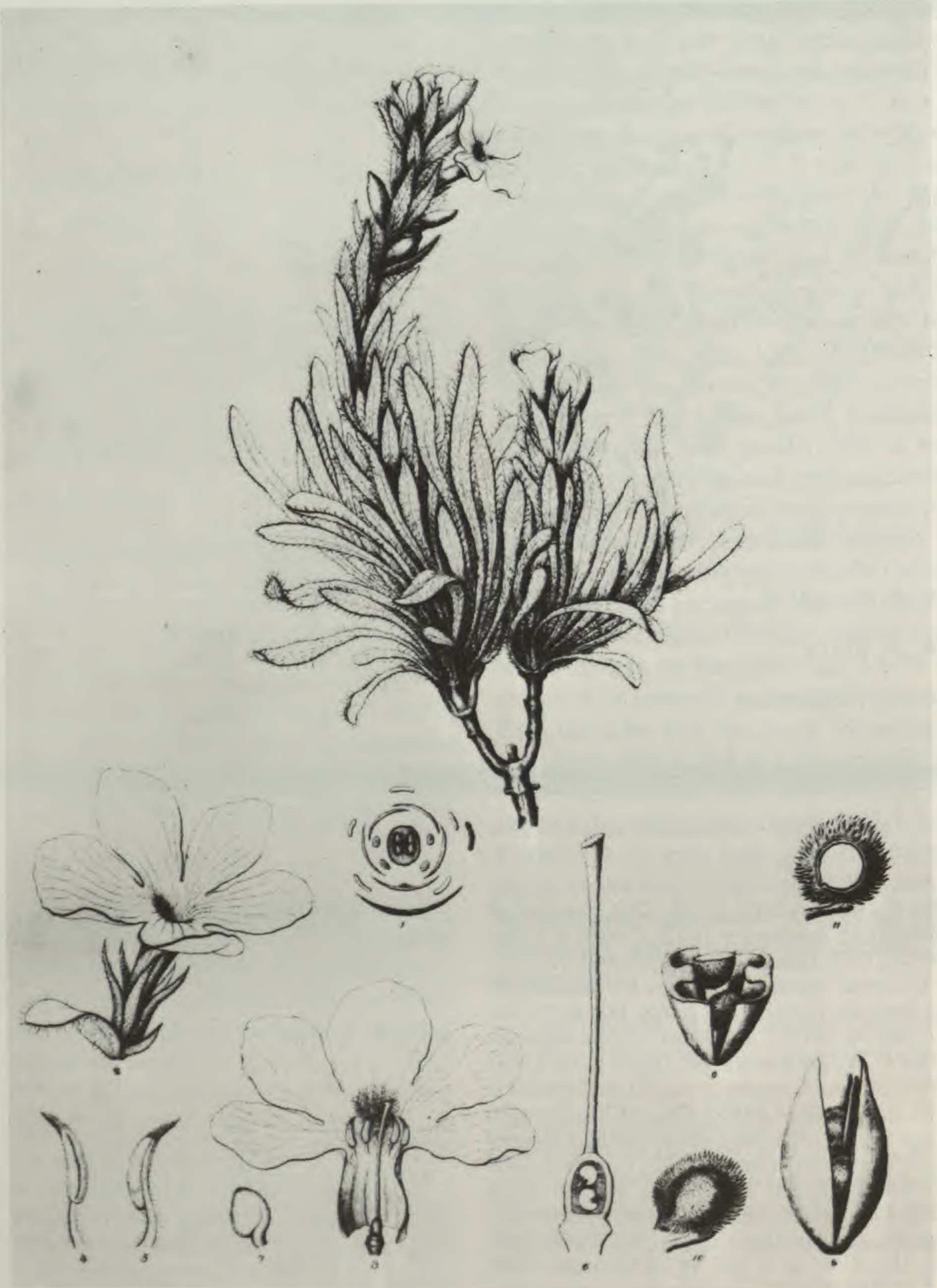


FIGURE 4. Illustration of *Stenandrium barbatum* from John Pope's report to the War Department in 1855.

spicuously pubescent with long (1–4 mm) stiff trichomes, leafy-bracteate spikes, and golden seminal trichomes that usually have recoiled lateral barbs or branches.

5. *Stenandrium chameranthemoideum* Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854: 139. 1854. TYPE: Mexico. Veracruz: Colipa, Mar. 1841, *F. Liebmann*

10750 (lectotype, C!, here designated; isotype, US!). *Gerardia chameranthemoidea* (Oerst.) Blake, Contr. Gray Herb. 52: 100. 1917.

Caulescent perennial herb to 3 dm tall. Stems terete to subquadrate, pubescent with an understory of straight to retrorse trichomes 0.05–0.1 mm long and an overstory (sometimes sparse or absent) of flexuous trichomes 0.5–1 mm long or

evenly pubescent with straight to retrorse trichomes 0.1–0.6 mm long. Leaves opposite, petiolate, the petioles 3–40 mm long, the blades ovate to elliptic to obovate, 16–82 mm long, 10–41 mm wide, 1.1–2.6 times longer than wide, attenuate-decurrent at base, rounded to acute at apex, the surfaces pubescent, sometimes sparsely so, the margin entire to irregularly undulate to subcrenulate. Inflorescences of axillary or terminal spikes to 10 cm long, the spikes sessile or borne on peduncles 2–15 mm long, the peduncles and spike axes pubescent like the stem or nearly glabrous, the flowers subopposite to alternate along the spike axes. Bracts lance-subulate to subulate, 2.5–7 mm long, 1–1.5 mm wide, the abaxial surface pubescent, the margin ciliate (or bracts very sparsely pubescent with short trichomes). Bractlets lance-subulate, 2–4 mm long, 0.5–0.7 mm wide, pubescent like bracts. Calyx 4–9 mm long, the lobes subequal, lance-subulate, 4–8.5 mm long, pubescent like bracts or nearly glabrous, the margin sometimes with inconspicuous glands as well. Corolla pinkish or whitish, 10–14 mm long, the tube 5–8 mm long, the upper lip 3.5–6 mm long with lobes 3.5–6 mm long, the lower lip 5–7 mm long with lobes 4.5–6.5 mm long, the anterior lobe pubescent or glabrous on abaxial surface, the other lobes glabrous. Stamens 2–2.5 mm long, the anthers 1.5–1.8 mm long. Capsule 6–9(–13) mm long, glabrous. Seeds 1.5–3.5 mm long, 1–2.5 mm wide, the testa covered with papilla-like trichomes (restricted to the margin in some plants) mostly lacking barbs.

*Distribution.* Eastern and southern Mexico (Veracruz and Chiapas) in canyons and on ridges at elevations from 250 to 1,000 meters (Sept.–Apr.) (Fig. 1).

*Additional specimens examined.* MEXICO, CHIAPAS: 13 km N of Berriozábal near Pozo Turipache and Finca El Suspiro, *Breedlove* 31226, 39893 (CAS). VERACRUZ: Hac. de Sta. Barbara, *Liebmann* 10749 (C); 22 km de Palma Sola Rumbo a Plan de Las Hayas, *Nevling & Gomez-Pompa* 1026 (F); Zacuapan, *Purpus* 5573 (UC); Cousoquitla, Zacuapan, *Purpus* 8202 (GH, MO, NY, US); Pachuquilla, Puente Nacional, *Ventura A.* 7364 (ENCB, MICH).

In the protologue of *S. chameranthemoideum*, Oersted (1854) cited two of Liebmann's localities in Veracruz, "Ved Colipa og Hacienda de Sta. Barbara." There are specimens on four sheets representing Liebmann's collections of this species at C. Three are from Colipa and bear the number 10750. The other is from the Hacienda de Santa Barbara and is numbered 10749. The

lectotype is here designated as *Liebmann* 10750 (specimen mounted on three sheets).

Unfortunately this species is not well represented in herbaria. The few known collections suggest that there is considerable variation in pubescence of *S. chameranthemoideum*. *Nevling & Gomez-Pompa* 1026 contains three plants that differ markedly in pubescence of the stems, inflorescence axes, and bracts.

The plants from Chiapas differ from those collected in Veracruz by their cauline pubescence (evenly pubescent with straight to retrorse trichomes 0.1–0.6 mm long), somewhat longer capsules (8–13 mm), and testa ornamentation (papilla-like trichomes restricted to the margin). In all other characters, however, these collections closely resemble the more northerly ones.

The closest morphological relative of this species appears to be *S. nanum*. Both species have a caulescent habit, opposite leaves, and narrow bracts and bractlets. The distinctions between them are discussed under *S. nanum*.

#### 6. *Stenandrium pedunculatum* (Donn.-Smith)

Leonard, J. Wash. Acad. Sci. 32: 187. 1942. *Blechum pedunculatum* Donn.-Smith, Bot. Gaz. (Crawfordsville) 49: 457. 1910. TYPE: Guatemala. Zacapa: ca. 0.5 mi. on opposite side of river from Gualán, 15 June 1909, C. Deam 6277 (holotype, US!; isotypes, GH!, MO!).

Erect or procumbent caulescent perennial herbs to 50 cm tall from a stout woody rootstock or rhizome. Stems pubescent with an understory of straight to retrorse trichomes, 0.2–0.5 mm long, and an overstory of flexuous trichomes, 0.5–1.5 mm long. Leaves opposite, petiolate, the petioles to 20 mm long, the blades ovate-elliptic to obovate, 12–90 mm long, 7–45 mm wide, 2–3.5 times longer than wide, subtruncate to long-attenuate at base, rounded to subacute at apex, pubescent on both surfaces (often sparsely so), margin entire to crenulate, usually ciliate. Inflorescence an axillary or terminal, often somewhat head-like, pedunculate spike to 35 mm long, the peduncles (0.5–)1.5–5 cm long, the flowers opposite or subopposite along the rachis. Bracts obovate, 5.5–14 mm long, 2.5–7(–12) mm wide, pubescent like leaves. Bractlets subulate, 1.5–5.5 mm long, 0.3–0.7 mm wide, glabrous or sparsely pubescent. Calyx 3–6.5 mm long, the lobes lance-subulate, 2.5–5.5 mm long, glabrous to sparsely pubescent. Corolla pink to white, 10–19 mm long,

the tube 5–7 mm long, the upper lip 4–8 mm long, the lower lip 5.5–11 mm long, the lobes subequal, 4–10 mm long or lobes of the lower lip to 1.3 times longer than those of the upper lip, the lower-central lobe pubescent on abaxial surface. Stamens 1.5 mm long, the anthers 1 mm long. Capsule 5.5–8 mm long, glabrous or sparsely pubescent above the middle. Seeds 2–3 mm long, 1.5–2.5 mm wide, pubescent with long, bristle-like trichomes with lateral barbs or branches.

*Distribution.* Western and southern Mexico (Jalisco, Colima, Guerrero, and Chiapas) and northern Central America (Guatemala, Honduras, and Nicaragua) in forests, especially along streams, and on grassy slopes at elevations from near sea level to 1,350 meters (May–Dec.) (Fig. 1).

*Representative specimens examined.* MEXICO. CHIAPAS: Venustiano Carranza, above Finca Carmen, along rd. from Acala to Pugiltik, *Ton 2990* (F, LL, MICH, US); La Trinitaria, along rd. to Boqueron W of Hwy. 190 at point 18 km SW of La Trinitaria, *Breedlove 42253* (MO). COLIMA: ca. 16 mi. WNW of Santiago, *McVaugh 14972* (MICH), *15734* (MICH). GUERRERO: 20 mi. NE of Acapulco, *Barkely et al. 17M722* (TEX). JALISCO: Pueblo Careyitos, near Chameña, *Pérez J. 1739* (ASU). GUATEMALA. HUEHUETENANGO: Sierra de los Cuchumantes, between Santa Ana Hista and Netón, *Steyermark 51400* (F). JUTIAPA: vic. of Jutiapa, *Standley 75318* (F). ZACAPA: Sierra de las Minas, near electric plant of Río Hondo, *Standley 74009* (F). HONDURAS. CHOLUTECA: mountains near El Banquito, *Williams & Molina R. 10796* (F). EL PARAISO: Orillas del Río Lizapa, Llano de Lizapa, *Molina R. 3955* (F, MO). MORAZÁN: drainage of Río Yeguaré near San Francisco, *Molina R. 218* (F, GH), *Williams 15911* (DS, F, GH, MO). NICARAGUA. ESTELÍ: Cerro de las Animas, NE of Estelí, *Standley 20325* (F).

This widely distributed species exhibits considerable variation in stem length, bract size, and pubescence. Plants of *S. pedunculatum* are distinguishable from other Mexican species by their caulescent habit, opposite leaves, obovate bracts, and relatively short capsules. The specimens from Colima differ from some of the more southerly collections by their shorter (1–3 cm long) stems. In other characters, however, they are identical with the latter.

Leonard (1942) noted the similarities between *S. pedunculatum* and *S. mandioccanum* Nees of southern South America, the distinguishing characters being the pubescent capsules and densely retrorse-pubescent stems of the latter species. Examination of several specimens of *S. mandioccanum* from Brazil and Argentina re-

veals that these characters will not distinguish the two species. Several specimens of *S. pedunculatum* have pubescent capsules and the plants of *S. mandioccanum* that I examined all had strongly antrorse cauline trichomes. In fact, my cursory examination suggests that specimens referred to *S. pedunculatum* and *S. mandioccanum* may be part of the same species. Based on the few specimens of *S. mandioccanum* available to me, the distinctions in the following couplet serve to separate the taxa:

- a. Cauline trichomes uniform in length, antrorse; plants of southern South America .....  
..... *S. mandioccanum*
- b. Cauline trichomes consisting of an understory of straight to retrorse trichomes and an overstory of longer, flexuous trichomes; plants of southern North America and northern Central America .....  
..... *S. pedunculatum*

Perhaps these differences are more reflective of varieties of one species than separate species. Until *S. mandioccanum* and its relatives in South America have been thoroughly studied, however, it seems prudent to maintain these taxa at their present status and avoid possible future nomenclatural reductions.

7. *Stenandrium subcordatum* Standley, J. Arnold Arbor. 11: 48. 1930. TYPE: Mexico. Yucatán: Chichen Itzá, 3 June 1929, *J. Bequaert 20* (holotype, GH!).

Acaulescent perennial herb to 1 dm tall. Leaves petiolate, the petioles 10–57 mm long, pubescent with flexuous trichomes, the blades ovate to elliptic, 19–56 mm long, 13–24 mm wide, 1.2–2.9 times longer than wide, truncate to cordate (often asymmetric) at base, the blade not decurrent on the petiole, rounded to acute at apex, the surfaces pubescent, the upper surface sometimes pale green to whitish along the major veins, the margin entire to irregularly undulate, ciliate. Inflorescence a pedunculate spike to 100 mm long, the peduncles (5–)20–65 mm long, pubescent with flexuous trichomes 0.2–1 mm long, the flowers alternate to subopposite along the rachis. Bracts lance-subulate, 4.5–7 mm long, 0.5–1.5 mm wide, pubescent on abaxial surface, the margin ciliate. Bractlets subulate, 2.5–4 mm long, 0.5–0.7 mm wide, pubescent like bracts. Calyx 4–6 mm long, the lobes subulate, 4–5.5 mm long, pubescent like bracts. Corolla pinkish purple, 14–17 mm long, the tube 8–9 mm long, the upper lip 3.5–5 mm long with lobes 3–4 mm long, the lower lip 5–8 mm long with lobes 5–7.5 mm long, the

lower-central lobe sparsely pubescent to nearly glabrous on the abaxial surface. Stamens 1.5 mm long, the anthers 1.1 mm long. Capsule 5.5–8 mm long, pubescent (trichomes sometimes very sparse). Seeds 1.5–2 mm long, 1–1.5 mm wide, covered with hair-like papillae.

*Distribution.* Known only from the state of Yucatán in Mexico and the department of Petén in Guatemala (Fig. 1) where the plants grow in clearings, dense forests, and along dry arroyos (Mar.–July).

*Additional specimens examined.* MEXICO. YUCATÁN: Chichen Itzá, Valladolid rd., Lundell & Lundell 7511 (LL, MICH); Chichen Itzá, Steere 1451 (MICH); Tizimin, Swallen 2530 (MICH). GUATEMALA. PETÉN: Uaxactum, Bartlett 12283 (CAS, K, MICH, TEX).

This rarely collected species is readily distinguishable from other Mexican species of *Stenandrium* by its leaf blades which are truncate to subcordate at the base and not decurrent along the petiole. *Stenandrium subcordatum* also has a distinctly zygomorphic corolla, more suggestive of the corolla in species of *Holographis* than that of other species of *Stenandrium*, with the lobes of the upper lip only about one-half the size of those of the lower lip. Unlike the corolla in species of *Holographis*, however, the corolla of *S. subcordatum* has an upper lip divided nearly to its base with obovate lobes. The affinities of *S. subcordatum* are with *S. dulce* from which it can be distinguished by the above mentioned characters as well as its shorter and narrower bracts and shorter capsules.

Perhaps the closest morphological relative of this species is *S. lyonii* J. R. Johnston of Venezuela. Both species have ovate to elliptic, basally truncate leaf blades sometimes with a whitish or pale green coloration along the major veins on the adaxial surface. Although *S. lyonii* was originally described as acaulescent (Johnston, 1908), examination of the type reveals it to be subcaulescent with slight internodal elongation. Other specimens of *S. lyonii* examined from Venezuela are conspicuously caulescent. These species can be distinguished by the following couplet:

- a. Plants subcaulescent to caulescent; bracts (6–) 7–10 mm long; bractlets 0.3–0.5 mm wide; corolla 8–13 mm long; capsule glabrous; plants of northern South America ..... *S. lyonii*  
 b. Plants acaulescent; bracts 4.5–7 mm long; bractlets 0.5–0.7 mm wide; corolla 14–17 mm long; capsule pubescent (sometimes sparsely so); plants of the Yucatán Peninsula ..... *S. subcordatum*

8. *Stenandrium pilosulum* (Blake) T. F. Daniel, comb. nov. *Gerardia pilosula* Blake, Contr. Gray Herb. 52: 101. 1917. TYPE: Mexico. Chihuahua: vicinity of Madera, 27 May–3 June 1908, E. Palmer 317 (holotype, GH!; isotype, US!).

Acaulescent perennial herb to 7.5 cm tall from a woody rhizome, the rhizome bearing numerous fleshy roots along its length. Leaves (plants often leafless or nearly so at anthesis) ascendant, petiolate, the petioles to 15 mm long, the blades oblanceolate to narrowly elliptic to lanceolate (to ovate), 11–30 mm long, 3–7(–10) mm wide, 2.8–4.7 times longer than wide, attenuate to decurrent at base, acute to rounded at apex, the margin entire, eciliate, the surfaces glabrous (although the lower surface inconspicuously glandular along the basal portion) and punctate-pitted. Inflorescence consisting of pedunculate spikes to 30 mm long, the peduncles 5–35 mm long, nearly glabrous or pubescent with retrorse to erect trichomes 0.05–0.2 mm long, the flowers opposite to subopposite along spike axis, sessile. Bracts ovate to narrowly elliptic to obovate, 6–11 mm long, 1.5–4.5 mm wide, pubescent like peduncles although the trichomes more numerous and the margin inconspicuously ciliate with trichomes 0.05–0.3 mm long. Bractlets linear to linear-lanceolate, 6–10 mm long, 0.5–1 mm wide, pubescent like bracts. Calyx 7–14 mm long, the lobes linear-subulate to linear-lanceolate, subequal, 6.5–13.5 mm long, pubescent like bracts. Corolla purplish, 10–23 mm long, the tube 6–15 mm long, the upper lip 3–8 mm long, the lower lip 4–8.5 mm long, the lobes subequal, 3–7.5 mm long, the lobes and tube glabrous or sparsely pubescent on the abaxial surface, the lower-central lobe often densely pubescent. Stamens 2.5–3 mm long, the anthers 1.5 mm long. Capsule 9–12 mm long, pubescent over the entire surface. Seeds 3–4 mm long, 3–3.5 mm wide, densely pubescent with long, bristle-like trichomes bearing lateral barbs or branches.

*Distribution.* Sierra Madre Occidental of western Chihuahua and eastern Sonora (Fig. 3) on gravelly slopes in pine-oak associations at elevations from 1,720 to 2,250 meters (Mar.–May).

*Additional specimens examined.* MEXICO. CHIHUAHUA: 4 mi. S of Guerrero, Correll & Johnston 21612 (ASU, LL, NY, US); 2 mi. E of Yepachic, Spaulding 75-3-58 (ARIZ). SONORA: ca. 5 mi. W of Yécora, Hubbell s.n. (ARIZ); 7 mi. NW of Yécora, Moran et al. 21965 (ENCB).

This little known species was described by Blake (1917) as *Gerardia pilosula* based on a single collection from Chihuahua. Recent collections have been either unidentified or misidentified. Plants of *S. pilosulum* are readily recognized by their diminutive stature and ascendant, glabrous (though inconspicuously glandular) leaves (which are often absent at anthesis). Although its affinities to other species were not noted in the protologue, it is morphologically similar to *S. dulce*, from which it can be distinguished by the following couplet:

- a. Plants leafless at anthesis or leaves glabrous; bracts not conspicuously ciliate, the margin pubescent with trichomes 0.5–0.3 mm long; bractlets linear to linear-lanceolate, tapering to apex from above the middle if at all; capsule entirely pubescent; plants restricted to the northern Sierra Madre Occidental of Sonora and Chihuahua ..... *S. pilosulum*
- b. Plants leafy at anthesis, leaves pubescent; bracts conspicuously ciliate, the trichomes (0.3–)0.5–2 mm long; bractlets subulate to lance-subulate, tapering to apex from at or below the middle; capsule glabrous or pubescent on upper half; plants occurring east and south of Sonora and Chihuahua ..... *S. dulce*

9. ***Stenandrium dulce*** (Cav.) Nees in DC., Prodr. 11: 282. 1847. *Ruellia dulcis* Cav., Icon. Pl. 6: 62, t. 585, f. 2. 1801. TYPE: Chile. Concepción: near Talcahuano, Née herbar. (not seen). *Gerardia dulcis* (Cav.) Blake, Contr. Gray Herb. 52: 101. 1917.

*Crossandra fascicularis* Benth., Pl. Hartweg. 22. 1839. TYPE: Mexico. Jalisco: Lagos, 1837, *T. Hartweg 182* (holotype, K!; isotypes, GH!, K!). *Stenandrium fasciculare* (Benth.) Wasshausen, Phytologia 12: 427. 1965.

*Stenandrium dulce* (Cav.) Nees var. *floridanum* A. Gray, Syn. Fl. N. Amer. 2(1): 327. 1878. TYPE: United States. Florida: Indian River, 1894, *E. Palmer 350* (holotype, GH!). *Stenandrium floridanum* (A. Gray) Small, Fl. Southeast U.S. 1st edition. 1085. 1903. *Gerardia dulcis* (Cav.) Blake var. *floridana* (A. Gray) Blake, Contr. Gray Herb. 52: 101. 1917.

*Stenandrium guatemalense* Leonard, Publ. Carnegie Inst. Wash. 461: 212. 1936. TYPE: Guatemala. Alta Verapaz: Cubilguitz, 1892, *H. von Turckheim 3588* (holotype, US!; isotypes, GH!, K!).

*Stenandrium mexicanum* Leonard, Kew Bull. 1938: 62. 1938. TYPE: Mexico. México: Temascaltepec, San Lucas, 7 July 1933, *G. Hinton et al. 4292* (holotype, K!; isotypes, ARIZ!, GH!, MO!, US!).

Acaulescent perennial to 20 cm tall from stout rootstock or rhizome. Leaves (sessile) petiolate, the petioles 5–65 mm long, the blades ovate

to ovate-elliptic (to oblanceolate to strap-shaped), 13–100 mm long, 4–44 mm wide, 1.5–5.5(–18) times longer than wide, rounded to acute to attenuate (to decurrent along petiole) at base, acute to rounded (rarely emarginate) at apex, the surfaces pubescent (rarely glabrous), usually glandular-punctate, the margin entire, crenulate, or somewhat irregularly undulate, flat to slightly revolute, ciliate or eciliate. Inflorescence a subsessile or pedunculate, head-like or usually elongate spike to 85 mm long, the peduncles 5–200 mm long, the peduncle and rachis pubescent with trichomes 0.1–1.5 mm long or nearly glabrous, the flowers sessile, alternate or opposite along the rachis. Bracts lanceolate to elliptic (rarely oblanceolate, obovate, or strap-shaped), (6–)9–20 mm long, 2–7.5 mm wide, usually conspicuously 3-nerved, the outer surface densely pubescent or glabrous, the margin ciliate with trichomes (0.3–)0.5–2 mm long. Bractlets lance-subulate to subulate, 3–9 mm long, 0.3–1(–1.5) mm wide, ciliate or eciliate, sometimes inconspicuously glandular along the margin. Calyx 4–11 mm long, the lobes lance-subulate, 3.5–9 mm long, often ciliate at tips and usually inconspicuously glandular along the margin. Corolla pink to purple, marked with white within, (10–)16–20(–27) mm long, the tube (6–)9–16 mm long, the upper lip 3–11 mm long with lobes 2.5–10 mm long, the lower lip 4–14 mm long with lobes 3.5–11 mm long, the lower-central lobe usually pubescent on abaxial surface, the other lobes mostly glabrous. Stamens 1.5–2.5 mm long, the anthers 1.2–1.5 mm long. Capsule 6.5–12 mm long, glabrous or sparsely pubescent above the middle. Seeds 2.5–4 mm long, 2–3 mm wide, pubescent with long, appressed, bristle-like trichomes bearing flexuose or downward-pointing lateral barbs or branches.

*Distribution.* Southern United States (Florida and Texas), Mexico (Aguascalientes, Chihuahua, Coahuila, Durango, Hidalgo, Jalisco, México, Michoacán, Nayarit, Nuevo León, Oaxaca, Puebla, San Luis Potosí, Sinaloa, Tamaulipas, and Zacatecas), Guatemala, Colombia, Ecuador, Peru, Chile, Bolivia, and Argentina. Plants in Mexico and adjacent regions (Fig. 3) occur in arid associations (with *Opuntia*, *Larrea*, *Condalia*, *Berberis*, *Flourensia*, *Yucca*, and *Parthenium*), grasslands, deciduous thorn-forest, and pine-oak communities at elevations from 20 to 2,700 meters. In Florida, the species occurs in seasonally wet pinelands (Feb.–Oct.).



FIGURE 5. Illustration of *Stenandrium dulce* from A. J. Cavanilles's "Icones et Descriptiones Plantarum," published in 1791.

*Representative specimens examined.* UNITED STATES. FLORIDA: Citrus Co., just N of Homosassa Springs, *Eyles & Eyles* 8260 (GH); Collier Co., Fla. 846, Seminole Indian Reservation, *Lakela* 28987 (RSA); Dade Co., Biscayne Bay, *Curtiss* 1945 (GH, K, US); Highlands Co., Rt. 18, 5 mi. W of Childs, *Brass* 15363 (GH, US); Hillsborough Co., Old Memorial Highway, ca. 1.5 mi. from Rt. 580 NW of Tampa, *Lakela et al.* 25084 (GH, RSA), *Lakela* 25243 (GH); Lee Co., vic. of Fort Meyers, *Standley* 71 (GH, US); County undetermined, locality unspecified, *Simpson s.n.* 1889 (DS, US). TEXAS: Hidalgo Co., Santa Ana Natl. Wildlife Refuge, *Fleetwood* 7007 (TEX); Starr Co., Hwy. 4, E of Fort Ringgold, *Runyon* 3256 (TEX); Webb Co., Rio Grande, Laredo, *Palmer* 1005 (GH, K); Willacy Co., ca. 4 mi. NNW of headquarters, *Sauz Ranch*, *Johnston* 53266.6 (TEX). MEXICO. AGUASCALIENTES: 30 km al W de Aguascalientes, *Rzedowski* 14020 (ENCB). CHIHUAHUA: 14 mi. SE of Rancho La Gloria on rd. to Cerros Blancos, 27°15'40"N, 104°09'W, *John-*

*ston et al.* 9003 (LL, MEXU). COAHUILA: Sierra del Pino, *Johnston & Muller* 393 (GH, LL); vic. of Saltillo, *Palmer* 529 (US), 578 (US). DURANGO: San Juan del Alamo, *Robert* 4024 (ENCB); ca. 12 mi. NW of Canatlán along Rt. 39, *Pinkava et al.* 9373 (ASU). HIDALGO: N of Jacala de Ledesma, *Clark* 7011 (MO). JALISCO: near rd. to León, Gto., 5 mi. SE of jct. at Lagos de Moreno, *McVaugh* 17798 (MICH); near Guadalajara, *Pringle* 11353 (GH). MÉXICO: Temascaltepec, Chorrera, *Hinton et al.* 754 (ENCB, GH, K, LL, MO, NY, US), 8080 (K, LL, MICH, NY, US); Peñon, *Hinton et al.* 6086 (F, GH, K, MO, NY, US). MICHOACÁN: Loma Santa Maria, vic. of Morelia, *Arsène* 2756 (US). NAYARIT: 23 mi. NNW of Tepic along Hwy. 15, *Marcks & Marcks* 1182 (LL); between Acaponeta and Pedro Paulo, *Rose* 3316 (US); 1-3 km W of El Venado along rd. from Ruiz to Jesús Maria, *Breedlove & Almeda* 45287 (CAS). NUEVO LEÓN: 1-2 mi. SW of Pabllillo, *Correll & Johnston* 19928 (LL, US). OAXACA: 28 km NW of La Ventosa along Trans-Isthmian Hwy., *King*

636 (MICH). PUEBLA: vic. of San Luis Tultitlanapa, near Oaxaca, *Purpus* 3340 (F, MO, UC). SAN LUIS POTOSÍ: Bagre, Minas de San Rafael, *Purpus* 5229 (F, MO, UC, US). SINALOA: between Concepción and Rosario, *Rose* 1534 (US); between Rosario and Colomas, *Rose* 3179 (US). TAMAULIPAS: 2 mi. S of Marcella, between Peña Nevada and Hermosa, *Stanford et al.* 2522 (DS, US). ZACATECAS: 6.5 mi. from San Tiburcio on rd. to Concepción del Oro, *Johnston* 2612 (TEX). STATE UNDETERMINED: locality unknown (probably Nayarit or Sinaloa), *Sessé et al.* 2174 (MA). GUATEMALA. PETÉN: Chiche, Petén, *Lundell* 3707 (F, MICH).

*Stenandrium dulce* (Fig. 5) is the most widely distributed species in the genus and the most morphologically variable. Plants from North and Central America show considerable variation in height, pubescence, leaf form, size of the corolla, bract shape, and density of flowers in the inflorescence. Several species have been described or proposed based on some of the diverse forms of *S. dulce*. Leonard (1936) described *S. guatemalense* and distinguished it from related Mexican species by its narrow, sharply acuminate, and pilose bracts. Later (Leonard, 1938), he described *S. mexicanum* and characterized it by broad leaf blades, obtuse or rounded bracts, and large purple flowers. He noted its close relationship to *S. dulce* from Chile. Gibson (1974) included *S. guatemalense* within *S. dulce* in her treatment of the Acanthaceae of Guatemala and *S. mexicanum* is here included in this common species. In 1932 Leonard labelled several diminutive, small-leaved specimens of *S. dulce* from north-central Mexico with a manuscript name at US. Several specimens from Michoacán and an unusual form from west-central Mexico were likewise given manuscript names. Leonard obviously believed *S. dulce* to be a South American species and the various morphological entities from North and Central America to be worthy of specific status. Examination of a large number of specimens from throughout America leads me to conclude that all of Leonard's entities are part of a single morphologically diverse species that lacks consistent gaps among the various forms. Species with large ranges and considerable morphological variability are well known in several other genera of American Acanthaceae (e.g., *Aphelandra aurantiaca* (Scheidweiler) Lindley, *Carlowrightia arizonica* A. Gray, *Elytraria imbricata* (Vahl) Pers., *Justica carthagenensis* Jacq., *Ruellia geminiflora* H.B.K., and *Tetramerium nervosum* Nees).

One of the entities "recognized" by Leonard is worthy of some discussion. Specimens from

southern Sinaloa and northern Nayarit (*Breedlove & Almeda* 45287; *Marcks & Marcks* 1182; *Rose* 1534, 3179, 3316; *Sessé et al.* 2174) are rather distinctive by their long, narrow (3–18 times longer than wide), and strap-shaped or oblanceolate (rarely elliptic) leaves, long (100–200 mm) peduncles, and glabrous corollas. In addition, the bracts vary from emarginate to rounded to acute at the apex and the bractlets and calyces of these plants are frequently glabrous. In specimens of *S. dulce* from other regions the leaves are usually wide (1.5–3.5 times longer than wide) and ovate or ovate-elliptic; the peduncles are usually less than 100 mm long; the lower-central petal lobe is usually pubescent; the bracts are acute at the apex; and the bractlets and calyces are normally conspicuously pubescent. Further, most of the specimens from Sinaloa and Nayarit are from regions of deciduous thorn-forest (*Breedlove & Almeda* 45287 is from a savanna) whereas all other collections of *S. dulce* from west-central Mexico are from grassland communities at relatively high elevations. This assemblage may eventually prove worthy of varietal or specific status because of the minor morphological tendencies and apparent ecological and geographical distinctness. The general overlap of all of the characters mentioned above between these plants and more typical specimens of *S. dulce* preclude formal taxonomic recognition of this assemblage until the variation from throughout the range of *S. dulce* has been considered. Indeed, some plants of *S. dulce* from Florida (e.g., *Simpson s.n.*, 1889) closely resemble the specimens from Sinaloa and Nayarit.

Asa Gray (1878) recognized *S. dulce* var. *floridanum* on the basis of glabrous plants with only the upper bracts and bractlets lightly hirsute-ciliate. Long (1970) noted the very similar appearance of *S. dulce* var. *floridanum* with *S. dulce* var. *dulce* and claimed the former differed by usually having the upper bracts and bractlets glabrous or sparingly hirsute-ciliate rather than hirsute. This distinction does not hold up when specimens from throughout the range of the species are examined. Long further noted the close relationship of this variety with *S. mexicanum* and the relationship between *S. faciculare* and *S. dulce*. Most of the variation encountered in *S. dulce* in the region covered by this revision can be seen among the diverse specimens from peninsular Florida.

The various forms comprising *S. dulce* are held together by a suite of characters including the

acaulescent habit, usually conspicuously petiole leaves lacking long (1–4 mm), white, shaggy trichomes, and lanceolate to elliptic (rarely obovate or strap-shaped) bracts. Several Mexican species, including *S. pilosulum* and *S. barbatum*, appear to be closely related to or even derived from *S. dulce*. These latter species are restricted to northern Mexico and adjacent regions of the United States, north and west of the range of *S. dulce*. The ranges of these three species are not known to overlap. The distinctions among them are summarized in the key and are further discussed elsewhere in the text.

#### EXCLUDED TAXA

*Stenandrium pelorium* Leonard, *Wrightia* 2: 83. 1960. = *Holographis peloria* (Leonard) T. F. Daniel, *Madroño* 31: 90. 1984.

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NOTE ADDED IN PROOF: After this revision went to press, a chromosome count of  $n = 26$  was obtained for *S. barbatum*. Relationships among *Stenandrium*, *Holographis*, and *Aphelandra* are discussed further by Daniel et al. (*Syst. Bot.* 9: 346–355. 1984) based on known chromosome counts of species in these genera.